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On the treatment of *Merendera* and *Bulbocodium* (*Colchicaceae*) as separate genera

Abstract

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Independence of the genera *Merendera* and *Bulbocodium* has been discussed for almost a century. In recent studies the monophyly of the genus *Androcymbium* has been questioned as well. This work attempts to analyze peculiarities of the geographic distribution, ecology, flower morphology (the structure of the stamens and stillodia), and chromosome numbers of the species of *Merendera* and *Bulbocodium*. The data obtained by this study are farther compared to the published data on the genera *Colchicum* and *Androcymbium*.

As a result of this investigation new important distinctions among the questionable genera were found. Most important are the evolutionary trends in their pollination system, such as intensification of the tendency toward cross pollination across entire species range of the questionable genera. This trends was likely connected to the secondary development (or preservation) of their apopetalous corolla. It defined peculiarities of the genera *Merendera* and *Bulbocodium*, their ecological niche preferences, dispersal abilities, developmental features and speciation. On the basis of these findings the author concludes that the status of *Merendera* and *Bulbocodium* should be preserved and they should be recognized as independent genera.

Key words: *Colchicum*, *Androcymbium*, taxonomy, *Liliales*.

Introduction

A discussion on the taxonomical position of the genera *Merendera* and *Bulbocodium* began since the publication of Stefanof (1926), who merged these genera with the genus *Colchicum*. Recent molecular data (Hoya & Pedrola-Monfort 2006, 2008; Manning & al. 2007; Persson & al. 2011; Vinnersten & Manning 2007) questioned the monophyly of the African genus *Androcymbium*, closely related to those genera.

Some morphological and anatomical peculiarities of these genera were studied by Oganezova (2002, 2004, 2007, 2008, 2011b) with the aim of defining boundaries of the genus *Colchicum* and a better placement of their questionable species. These works also include correlated analyses of geographic and ecological peculiarities, chromosome numbers, and morphology of stamens and styles of the species of *Colchicum*. These particular features were selected for this study because species of *Colchicum* reveal a correlation between slight macro-morphological variations to cer-

tain variability in the generative sphere, probably connected to pollination peculiarities. Chromosome numbers and ploidy levels are also variable in different parts of the geographic range of the genus *Colchicum*.

Material and methods

This work presents analytical data on the genera *Merendera* and *Bulbocodium*, their comparisons with those for the genus *Colchicum*, as well as with the recently published data on the genus *Androcymbium*. The data on geographical distribution, ecological peculiarities, flower morphology, and chromosome numbers of all 20 species of the genus *Merendera* and 2 species of the genus *Bulbocodium* where the same way as for the genus *Colchicum s.str.* (Oganezova 2011a) obtained. Several tentative species were included to this analysis on the basis of their treatment in the above mentioned morphological and anatomical works; their data can argue against the treatment of those species as synonyms.

Colchicum ignescens Perss. (Persson 2007) which, according to the author's description, has no flower tube (apopetalous corolla), the latter being a basal trait distinguishing species of *Colchicum* and *Merendera*, is treated here as the species of genus *Merendera*. Almost all species of *Merendera* and *Bulbocodium* are synanthous with leaves and flowers emerging simultaneously in the spring or late winter. Only two species – *M. filifolia* and *M. montana* (syn. *M. pyrenaica*) flower at the end of summer or early autumn while their leaves only start emerging during flowering period. Stefanov (1926) named such species sub-synanthous (*M. filifolia*) or sub-hysteranthous (*M. montana*).

Most of the data for our analysis come from the literature: Brotero (1804), Coste (1906), Stefanof (1926), Chernjakhovskaja (1935), Grossheim (1940), Vvedenskij (1963), Otchiauri (1963), Valentine (1980), Valdés (1980), Brikell (1984), Wendelbo (1985), Gabrielian (1985, 1986, 1999, 2001), Valdés & al. (1987), Persson (1992, 2007), Varol (2005), Melnik, al. (2007). For the chromosome numbers we also used: Darlington, Wilie (1955), Zakhariyeva, Makushenko (1969), Fedorov (1969), Moore (1973), Pogosyan (1981, 1997), Bokeria (1988, 1999), Takhtajan (1990), Goldblatt (1990), Goldblatt, Johnson (1991, 1996), Magulaev (1992), Nazarova, Gukasyan (2004), Persson (2009).

Analyzed characters are summarized in the Tables 1 (genus *Merendera*) and 2 (genus *Bulbocodium*). The species in the Table 1 are grouped according to their geographical ranges in the following geographic regions: the Eastern Mediterranean, Western Mediterranean, Central Asia, and the Armenian Highland with adjacent territories. The latter including the Great Caucasus, Transcaucasia and western parts of the Iranian Highland. One or two species of *Bulbocodium* (*B. versicolor* being dubious) are found in the Eastern Mediterranean extending to the Western Mediterranean (Persson 2007). Species authorities and synonyms are listed in the Tables 1 and 2.

Results

Genus *Merendera*. – Major peculiarities of the species of the genus (Table 1) are as follows. Their distribution is limited (Maps 1, 2) to comparatively narrow strip extending from Western Himalayas to the Pyrenean Peninsula and North-Western Africa, a typical Mediterranean-Frontal Asian range. All species inhabit open communities from lower to upper elevations in the mountains. The highest concentration of species with variable morphology, ecology, and basic chromosome numbers is found on the Armenian Highland and adjacent territories. This region has eleven diploid species including six species with basic number $x = 9$ (10), two species of each with basic number

Table 1. Genus *Merendera* Ramond species.

Species	Distribution	Habitat	Anthers fixation type and size (mm)	Style	Stigma	Flower/ Fruit	Chromosome number	
							<i>x</i>	<i>2n</i>
I. W Mediterranean								
<i>Merendera androcymbioides</i> B. Valdés	Spain -Andalusia, (endemic)	Low belt, dry places	Basal 3-4 (-5)	=/ <	Punctif.	III/ VI?	9	54
<i>M. filifolia</i> Cambess	NW Africa, S Portugal, Spain, Balearic islands, SE France	Dry places, sandy soil. Low mountain belts	Basal (5.5) 8-12 (17)	>/ =	Punctif.	IX-XI/ II-IV?	9	54
<i>M. montana</i> (L.) Lange	Pastures in C Perinea (Fr., Sp.), N Portugal	Dry places, limestone hills, from low to middle mountain belts	Basal (5.5-) 8-12 (-17)	>	Punctif.	VIII-X/ V-VI	9	54/60 (54+0-6B)
II. E Mediterranean								
<i>M. attica</i> (Spruner) Boiss. et Spruner (<i>M. rhodopea</i> Velen.)	Bulgaria, Greek, E Aegean island, W Turkey	Open dry stony places / 200-2000 m	Dorsal 1.5-3	>/ =1	Punctif.	XII-III/ V?	9	54
<i>M. sobolifera</i> Fish. & C.A. Mey.	From Balkan penisl. across SW Asia, Caucasus to C. Asia	From dry or marshy places in low belt to melting snow; 800-2400 m	Dorsal 1.5 (-2) -3.5 (-4)	>/ =	Punctif.	III-IV/ VI	9	42, 54
<i>M. figalii</i> Varol.	SW Turkey (endemic)	Open stony places, serpentine rocks. 1900-2100 m	Dorsal ?	>1	Punctif.	V/?	9	54

Table 1. continued.

III Armenian highland and neighboring territory									
<i>M. manissadjunii</i> Azn.	N Anatolia, Armenia	On meadows, moist places. 1000-3000 m	Dorsal 4	=/ >	Weakly oblique	IV-VI/ VIII	11	22	
<i>M. mirzoevae</i> Gabr.	Armenia (endemic)	Dry stony places, shibljak. (meadows). 700-1000 (2300) m	Dorsal 4-6	>/↓	Punctif.	I-II/ IV-V	9	18	
<i>M. greuteri</i> Gabr.	Armenia (endemic)	Tragacant steppe. 1500-1700 m	Dorsal 2-2.5	> / 1	Punctif.	IV-V /V-VI	?	?	
<i>M. candidissima</i> Mischez. ex Grossh.	S Transcaucasia, Talish	Tragacants, open forest with Juniperus species, dry stony places. 400-1800 m	Dorsal 4	> / = 	Punctif.	I-IV/ IV-V	9	18	
<i>M. eichleri</i> (Regel) Boiss.	E Ciscaucasia, Dagestan, E Transcaucasia	Dry, sandy places, grassy slope. Up to 1200 m	Dorsal 3-4	> 1	Punctif.	II-IV /IV-V	9	18	
<i>M. ghalgana</i> Ochiauri	C & E Caucasus (endemic)	Subalpine, alpine meadows, near melting snow. Alt. 2400 m	Basal 3 (-3.5)	=	Punctif.	V / VII?	12	24	
<i>M. raddeana</i> Regel	C, SW Caucasus, SW, S Transcaucasia, Karabakh, E Turkey, NW Iran	Subalpine, alpine turf meadows, near melting snow. Alt. 2100-3400 m	Dorsal 2	> / = / < 1	Punctif.	IV-V/ VI-VII	9	18, 20	
<i>M. trigyna</i> (Steven ex Adam) Stapf	E Ciscaucasia, Transcaucasia, E Turkey, NW Iran	Dry stony places, mountain steppe. Alt. 800 – 2200 m	Dorsal 2-3	> / < ↓ / 1	Punctif.	II-IV / V-VII	9	18, 20	
<i>M. wendelboi</i> (K. Perss.) Oganezova	W Iran (endemic)	On rocky or alluvial soil near melting snow. Alt. 2000-3000 m	Dorsal (2.5-) 3-4	> / =	Punctif.	II-V / ?	12	24	

Table 1. continued.

<i>Colebitum ignescens</i> K. Perss. (free tepals)	SE Turkey (Urfá, endemic)	Mountain slope, volcanic soil. Alt. 1500-1700 m	Dorsal (2.5-) 3-3.8	=/<?	Punctif.	III-IV/V	11	22
<i>M. kurdica</i> Bornm.	SE Turkey, W Iran, NE Iraq	Meadows, subalpine meadows, among cushion shaped needle. Alt. 1650 (Iran)-3000 m	Dorsal. 3-5	=/>	Punctif.	V-III/VII -...	9	18, 20
III. Central Asia								
<i>M. robusta</i> Bunge	N, NE Iran, C Asia to W Himalaya	From desert to high mountain steppe. Alt. 200-4500 m	Basal (3-) 4-16 (-18)	=/<? /h	Punctif.	II-III/VI	9	54
<i>M. hissarica</i> Regel	Pamir-Alai (endemic)	Alpine belt, near snow. Alt. 2000-4000 m	Basal 5-6 (-8)	</>	Punctif.	VI/VII-VIII?	9	54
<i>M. jolanthae</i> E. Czermiak.	SW, C Kopetdag (endemic)	Clay slope, gypsum hills. Middle & high mountain belts	Dorsal 8-9 (-13)	>	Punctif.	III-IV/?	9	36

Abridgements & symbols: N – north, E – east, W – west, S – south, C – central; Fr. – France, Sp. – Spain, punctif. – punctiform stigma; > - style longer than anthers, < - style shorter than anthers, = - style equal to anthers, / - or, flower. - time of flowering, fruit. - time of fruiting, || - strait style, 1 - top of style weakly oblique, ? - unknown.

Table 2. Genus *Bulbocodium* L. species.

Species	Distribution	Habitat	Anthers fixation type and size (mm)	Style	Stigma	Flower/fruit	Chromosome number	
							x	2n
<i>Bulbocodium vernum</i> L.	Perinea, W Alps (Fr., Switzer., It., Austria)	Meadows. Alt. 500-2000 m	Dorsal 3-4	>	Punctif.	III-V/?	11	22
<i>B. versicolor</i> Ker Gawl.	SE, C Europe	Steppe, forest-steppe	Dorsal 3-3.8	>	Punctif.	III-IV/?	11	22

Abridgements & symbols are the same as for Table 1: Switzer. – Switzerland, It. – Italy.

$x = 11$ and 12 . Most species in this region have anthers dorsally fixed to the filament. Only *M. ghalgana* has basal fixation with the connective so short, that anthers are partially mobile.

All the species of this region have stait styles with sometimes slightly bent apex. The stigmas are punctiform. They can rarely be of a slightly descending type. Both *Colchicum* and *Merendera* exhibit variability in the proportions of the style and stamen length. They can be of equal length, or longer, or shorter in relationship to each other. Populations of some species have all possible varieties. *M. trigyna* and *M. mirzoevae* have more or less reduced styles, which is a tendency towards formation of mail flowers.

The three eastern Mediterranean species of *Merendera* are morphologically similar with the species of Armenian Highland and adjacent territories. They have less variability in the characters in subject. All of them have dorsally fixed anthers of similar length and punctiform styles. These are polyploid species with basic number of chromosomes $x = 9$ and prevailing number $2n = 54$.

There are three species in the eastern part of the genus area, in Central Asia. Two of these, *M. jolanthae* and *M. hissarfica* are considered to be questionable by the genus monograph Persson (1992, 2007, 2009). Cultivars of *M. jolanthae* in Göteborg Botanical Garden collected from the *locus classicus* in Kopet Dagh Mountains were treated by Persson as *M. robusta* with chromosome number in all specimens $2n = 54$, as opposed to $2n = 36$ for *M. jolanthae*, published by Zacharjeva, Makushenko (1969). Only the status of *M. robusta* is not questionable. Because of limited availability of the material for this study I cannot decide if *M. jolanthae* and *M. hissarica* deserve a species rank. But they are treated here as independent species due to differences found in the structure of their leaves, nectaries and connectives (Oganezova 2002, 2004 a, b).

M. robusta and *M. hissarica* have large basifixed anthers, whereas the specimen of *M. jolanthae* studied by me has dorsal anthers. The proportions of style and anther length are variable. Central Asian species are polyploids – hexaploids (and tetraploids?), with only one basic chromosome number $x = 9$. Westernmost parts of the genus range have three species with absolute predominance of hexaploids with basic chromosome number $x = 9$, $2n = 54$ and decreased variability in all discussed characters.

In the species description for *M. androcymbioides* Valdés (1978) describes basifixed anthers which agrees with my data (Oganezova 2002). Judging from the photograph of the herbarium specimen in the description one could see a similar type of anther fixation to that in *M. ghalgana*. In “Flora vasculare de Andalucia Occidentale” Valdés (1987) describes these anthers as subdorsal. The author was probably describing a short connective which makes the anthers somewhat flexible. Another peculiarity of the western Mediterranean species is a tendency towards hysteranthous leaves typical for *M. filifolia* and *M. montana*.

It should be specifically noted that for the species in western and eastern parts of the genus range basally fixed anthers correlate with the sharp increase in their length. For example the anthers of *M. filifolia* and *M. montana* range from 5.5 to 17 mm, and those of Central Asian species from 3 (-4) to 16 (-18) mm. In all the other species they only range in the boundaries of 2-3-4 mm under dorsal fixation. It is possible that on the margins of the genus area the presence of vertical large fixed anthers increases the probability of autogamy.

Genus *Bulbocodium*. – All species of *Bulbocodium*, no matter if the genus is monotypic or ologotypic, are ephemeroïds found in open habitats of Eastern Sub-Mediterranean (*B. versicolor*) and Western Mediterranean (*B. vernum*). The eastern species grows in steps and semi steps of Eastern Great Plains, whereas the western species *B. vernum* is a mountainous species of high and middle altitudes. They exhibit no sharp differences in the above discussed characters. They have dorsally fixed small anthers (3-4 mm), with stamens shorter than the style, which has a punctiform stigma. Both species are diploids with the basic number $x = 11$, $2n = 22$. Besides some ecological distinctions the species differ in only the width of their leaves. *B. vernum* has broader leaves (15×1.5 sm), than *B. versicolor* ($15 \text{ sm} \times 0.0.8$ sm). This might be connected to different humidity levels in the habitats of these species, which grows at different elevations.

Discussion

A comparison of our data regarding the species of *Merendera* and *Bulbocodium* with those on the species of *Colchicum* (Oganezova 2011a) reveals following characteristics.

Geographic areas of all the three genera are similar, but species of *Merendera* have their center of diversity, and probably of origin, on the Armenian Highland and adjacent territories. Here are found the diploid species with different basic chromosome numbers $x = 9$ (10), 11, 12. Other parts of the genus range have only polyploids with basic chromosome number $x = 9$. Stamen morphology of the species of *Merendera* from the Armenian Highland and adjacent territories shows all varieties of anther to filament fixation types, relative length of styles and stamens, and styles shape. Some species have a tendency to form male flowers. They grow in various habitats and at different altitudes with different periods of flowering from April (sometimes from January) to May, accordingly various fruit ripening periods.

Eastern Mediterranean species have similar morphological and other characters to those of the Armenian Highland, but their characters are not variable and the species are polyploids – $x = 9$, $2n = 54$ (42).

In the Central Asian part of the genus area the species are only slightly variable by flower morphology and two of them have large basifixed anthers. This species have parallel characters with the local species of *Colchicum* – *C. luteum* and *C. kesselringii* (Oganezova 2011a). Central Asian species of *Colchicum* also have basifixed large anthers, 4.5-17 (-20) mm, with proportions of stamen and styles length similar to those in species of *Merendera*.

Western Mediterranean species of *Merendera* stand out. They are also polyploids ($x = 9$, $2n = 54$) with basifixed very large anthers and can be equal length of styles and stamens. Their most interesting peculiarity is that two of the three species are autumn blooming with a tendency of being hysteranthous. Species of *Colchicum* from the same region are also hysteranthous and have large anthers and other characters in stamen and style structure favoring autogamy. Their polyploidy level reaches $24x$ (Oganezova 2011a).

This analysis brings me to the following conclusions. While for the species of the genus *Merendera* in the central part of the its area – Armenian Highland – a tendency towards cross pollination is dominant, close to its western and eastern boundaries we see subtle structural recombination which may make autogamy possible. This pollination type is more problematic for the species of the genus *Merendera* than those of the genus *Colchicum*.

Unlike *Merendera*, *Colchicum* has two centers with diploid species – in the South-East Mediterranean and on the Armenian Highland (Oganezova 2011a). For the species growing outside of these centers in other parts of the range, morphological characters are altered as follows: their stamens become longer than their styles, the latter may have curved tips, and the styles may have descending shape. Large basifixed anthers become very common (Oganezova 2011a). These characters coupled with the presence of the perianth fused into the flower tube, sharply increase a possibility of autogamy.

Besides some obvious similarities in the structure and biology of the species of *Merendera* and *Colchicum*, their main distinction is, probably, in fewer possibilities of autogamy for *Merendera*, which thus define the specificity of this genus. Interestingly, the ancestral genus *Androcymbium* has variable systems of sexual reproduction with different combinations of self-compatible and self-incompatible (Membrives & al. 2002). According to Membrives & al. (2001) the system of reproduction served as a vector in some period of evolution of this genus. This might have created the differences among its species and the reasons of the current discussion about its delineation.

1. Thus *Merendera* and *Colchicum* are well defined by their geographic ranges. *Merendera* has the only center of diversity of diploid species on the Armenian Highland and adjacent territories, whereas *Colchicum* has to two centers with diploid species – on the Armenian Highland and in south – South-East Mediterranean (Oganezova 2011a).

2. There are differences among these taxa in the flowering, vegetation, and fructification. *Merendera* has practically no hysteroanthous species. *Colchicum* has almost twice as many hysteroanthous species as synanthous.

3. There are three basic chromosome numbers among the species of *Merendera*: $x = 9, 11,$ and 12 . Sometimes $2n = 20$ is found among diploid populations with $2n = 18$ on the Armenian Highland. The typical for these species polyploidy is probably allo- or autopolyploidy on the basis of the only basic number $x = 9$. There are no known polyploids on the basis of other basic numbers. Among species of *Colchicum* polyploidy is based on several basic numbers. Persson & al. (2011) cite the following row of basic numbers: $x = 7, 8, 9, 10, 11, 12,$ as well as some vague numbers, possibly of the aneuploids.

4. In the flower morphology among the species of *Merendera* there is a slight tendency towards autogamy. Autogamy is also characteristic for species of *Colchicum*. The only morphological character, which may cause of autogamy in the species of *Merendera* is the basal fixation of large anthers. There are no other alterations in the flower morphology. The absence of the flower tube and the easy splitting of the perianth into tepals, sharply diminishes the possibility of anthers contacting the style. These differences in the geography, biology, morphology, and karyology among species of *Merendera* and *Colchicum*, in my opinion, may support the preservation of *Merendera* as a separate genus.

Genus *Bulbocodium* (Table 2) represents a similar case. It is a mono-(oligotypic) genus with which also has the area of distribution within the boundaries, but much more narrow, than that of the species of *Colchicum*. It stretches from the open xero-mesophytic plains in Sub-Mediterranean Eastern Europe to meso-xerophytic middle and high elevation mountain communities in Western Mediterranean. In the flower morphology of the species of the genus *Bulbocodium* there are no traits to be treated as adaptations to autogamy. The tepals are fused only at the base, being distinct above, there is no flower tube, the stamens are shorter than the stigma of the pistil, the anthers are not large, the styles are absent – there is only one style with a punctiform stigma. The basic chromosome number is $x = 11, 2n = 22$. This taxon may represent an evolutionary line towards cross pollination. It would be logical to recognize its independence as well.

The problem of relationships of these taxa was addressed in some recent molecular phylogenetic analyses. Vinnersten & Reeves (2003) studied phylogenetic relationships within *Colchicaceae* based on three plastid regions. They sampled many species of *Androcymbium*, seven species of *Colchicum* s. str. and *Bulbocodium vernum*. They also sampled three species of *Merendera*: *M. longifolia* Hutch., *M. schimperiana* Hochst., *M. montana*. A more recent work (Vinnersten & Manning 2007) included *M. schimperiana* and *M. montana*. According to Persson (2007) *M. longifolia* and *M. schimperiana* are synonyms of *Androcymbium schimperianum* (Hochst.) Perss. & Del Hoyo. The genus *Androcymbium* with the species distributed in the west and east parts of South Africa and in north part of Africa was found non monophyletic (Map 2) and splits on two groups. In the case if the species of *Androcymbium* are nested in the genus *Colchicum*, monophyletic condition of the genus will be supported. Similar results were obtained by Hoyo, Pedrola-Monfort (2006), Manning & al. (2007). In these works the number of sampled species of *Colchicum*, *Merendera*, *Bulbocodium* was restricted to two of each genus. Hoyo, Pedrola-Monfort (2006) explained the paraphyly of *Androcymbium* by its dispersal from South Africa to northern Mediterranean Africa by arid tract, which was formed at the end of Miocene. These authors are considering future restructuring the taxonomy and nomenclature of the tribe *Colchiceae*. Manning & al. (2007) redefined taxonomic and nomenclature of the genus *Colchicum* by inclusion of the genus *Androcymbium* in it.

A further work by Hoyo, Pedrola-Monfort (2008) included more cpDNA and nDNA regions, as well as morphological and life-history traits data in the analysis of the genera in question. The authors concluded that there is no reason to expand *Colchicum* to include *Androcymbium*, but inclusion of *Bulbocodium* and *Merendera* within *Colchicum* was supported.

Persson & al. (2011) studied mainly *Colchicum* s. l. (96 species) and used three species of *Androcymbium* and *Hexacyrtis dickiana* Dinter as outgroups. The analysis was based on 292 parsimony-informative characters, derived from nucleotide sequences from six chloroplast fragments and 33 morphological, life history traits, as well as chromosome numbers. The two data sets (plastid data; morphology) were analyzed separately and combined. The work was aiming to define subgenera and sections of *Colchicum*. The results of this work better agrees with some of the informal species groups defined by Persson (2007) in earlier publications, than Stefanov's (1926) taxa. The the cladogram based on molecular data the species of *Colchicum* s. l. are grouped into a large clade of species in *Colchicum* s. str. and a smaller one which, besides the species of *Merendera* and *Bulbocodium*, includes *C. luteum*, *C. kesselringii* in the same group with *M. robusta*, while *C. schovitsii* is allies with *C. raddeanum* (= *M. raddeana*) and *C. kurdicum* (= *M. kurdica*). The cladogram based on morphological traits was considerably more homoplasious than the one based on molecular characters, but it provided added resolution to the trees derived from combined analysis. In combined analyses of plastid sequences and morphological traits the inference places *Colchicum* as sister to the genus *Androcymbium*. Authors conclude that additional data will be needed to resolve all relationships.

Thus the origin and relationships of these taxa remain not completely clarified.

Such basal morphological character as free tepals of flower, which clearly defines species of *Merendera* and *Bulbocodium* from species of *Colchicum*, is traditionally considered as primitive.

Persson & al. (2011) agree with this by treating free tepalous perianth as plesiomorphic. This character is found in the species of the ancestral genus *Androcymbium*. *Merendera* and *Bulbocodium* species might have inherited this character from the ancestral group (Manning & al. 2007). However, such a conclusion is in odds with the geography, morphology, and cytology of the species of *Merendera* and *Bulbocodium*. The species ranges of these genera are far from south-eastern Mediterranean, where the two species of *Androcymbium* (Map 2) grow, and where there is a diversity of synanthous and hysteranous species of *Colchicum* with highest variability of flower morphology characters and diploid chromosome numbers. This region might be the center of origin of the genus *Colchicum* (Oganezova 2011a).

This is not the only part of Mediterranean where species of *Colchicum* and *Androcymbium* coexist. Some species of *Colchicum* are in the contact with the species of *Androcymbium* all along the northern Africa.

Ranges of *Merendera* and *Androcymbium* meet only in the western Mediterranean, where there are three species of *Merendera*, with clearly specialized characters (hexaploids with basic number $x = 9$, basifixed anthers, and some tendency towards hystercancy and very large anthers in the two species from that region).

One can doubt in the evolutionary significance of the intersection of the ranges of *Merendera* and *Androcymbium* in the western Mediterranean region. The authors who specified migrations of the species of *Androcymbium* from southern Africa to the north, into the Mediterranean (Caujapé-Castells & al. 2001; Hoyo, Pedrola-Monfort 2006), assume that the species spread from the eastern Mediterranean to the west, with local extinctions during the Pliocene-Pleistocene climatic deteriorations.

This east to west Mediterranean migration pattern of *Androcymbium* is based on the following. Molecular studies define all North African species as a monophyletic group that splits to two subclades. Subclade one includes *A. rechingeri* Greuter / *A. psammophilum* Sventenius / *A. hierrense* Santos / *A. wyssianum* Beauverd & Turrett, while subclade two has *A. palestinum* Baker / *A. gramineum* (Cav.) McBride. The basalmost position of *A. rechingeri* from Crete and *A. palestinum* from Israel, coupled with the weak relationships between *A. rechingeri* and *A. wyssianum* from Algeria and the Canarian species – *A. psammophilum* and *A. hierrense* – brought to a conclusion that the eastern Mediterranean species of *Androcymbium* branched earlier.

The fact that *Merendera* is not in contact with the basally branching in the Mediterranean species of *Androcymbium*, point to a possibility that distinct tepals in *Merendera* and *Bulbocodium* might be

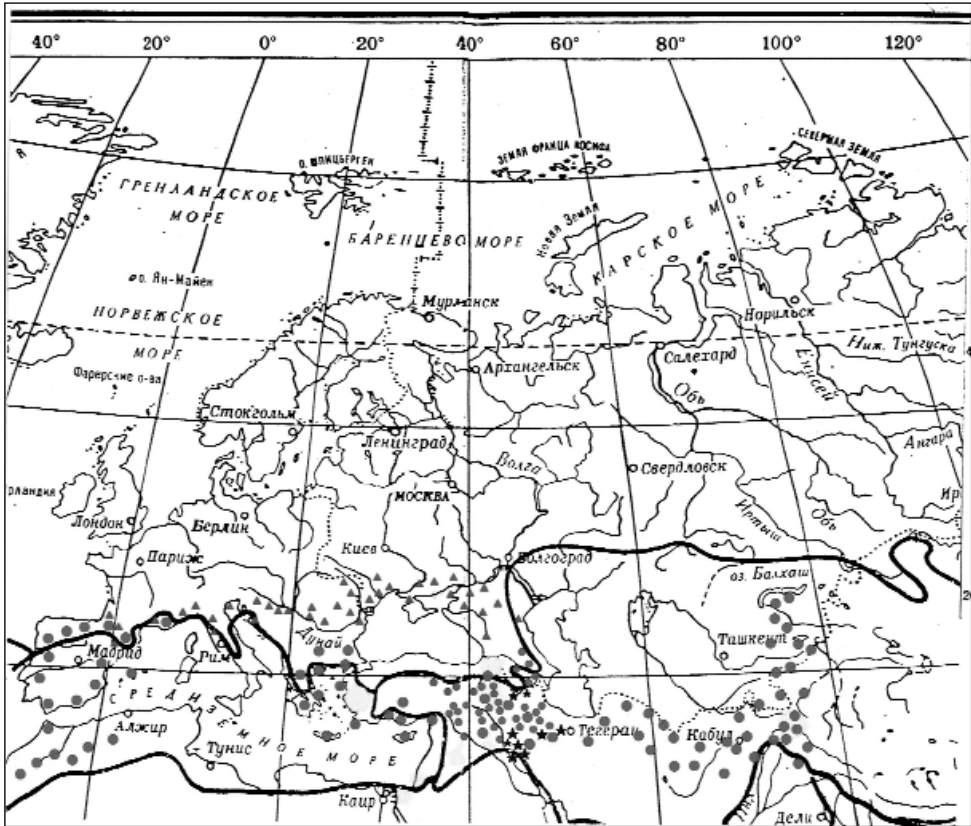


Fig. 1. The ranges of genera *Merendera* (circle, aster) and *Bulbocodium* (triangle).

The Base map is a fragment of the map from Takhtajan A. L monograph "Florističeskie oblasti Zemli" (1978). The greater size of circle is marked polyploid species of *Merendera* with $2n = 54$. The cytotypes accordingly are marked: by triangle – $x = 11$, by circle – $x = 9$, by aster – $x = 12$.

of a secondary origin. This character evolved in accord with the tendency towards cross pollination, which is peculiar for these two genera. The flowers of their species resemble a flower tube in the early developmental stages – many have special outgrowth and small pockets which hold the tepals together. After insect visitations this integrity is lost, and then own pollen is less likely to pollinate own styles and to compete with the pollen from other individuals.

Persson & al. (2011) indicate chromosomal reversals for this group of taxa – some species have reduced numbers of chromosomes – from hexaploidy to tetraploidy races. Is it possible that presence of distinct tepals is a reversal in the flower morphology?

Another character that defines *Bulbocodium* from *Colchicum*, is the type of style development in *Bulbocodium*. Persson & al. (2011) consider this character being negligible, because otherwise in molecular analysis the genera *Colchicum* and *Merendera* become paraphyletic.

It might be possible to find the ancestral forms for *Merendera*, *Bulbocodium* among synanthous species of *Colchicum*.

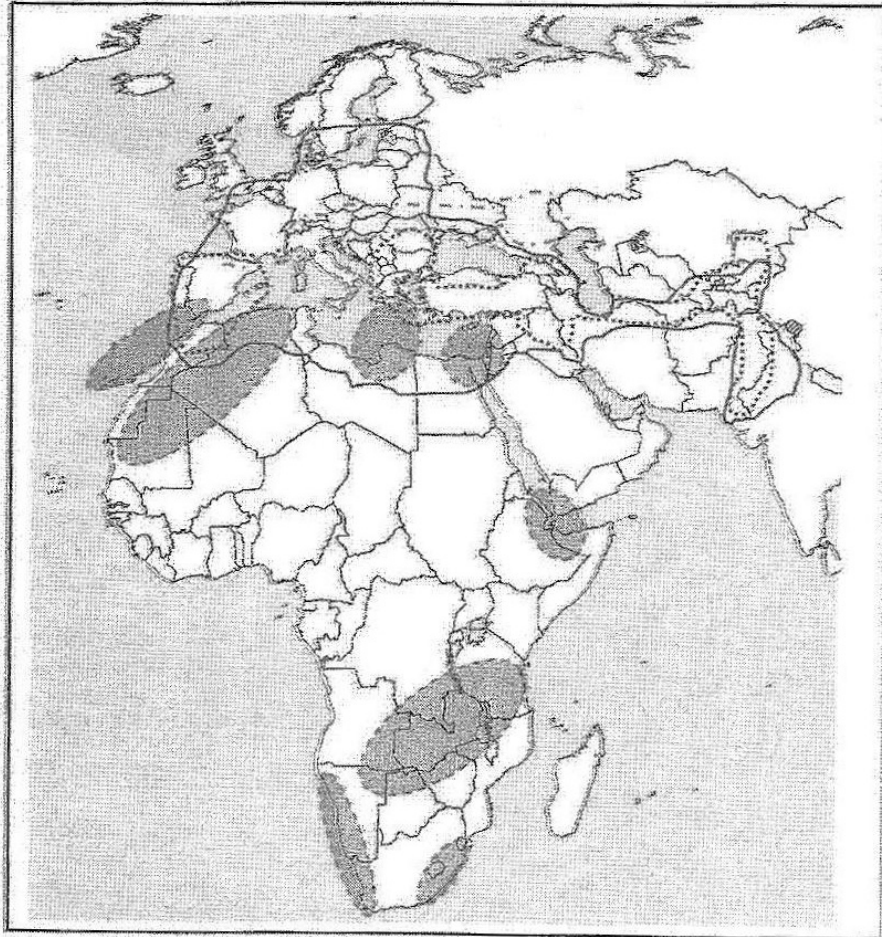






Fig. 2. Distribution of :  *Androcymbium* (no Caujape-Castells, & al., 2001);  *Colchicum*;  *Merendera*;  *Bulbocodium*.

Fig. 2. Distribution of *Androcymbium* (by Caujape-Castells & al. 2001), *Colchicum*, *Merendera* and *Bulbocodium*.

Conclusion

Available the data molecular phylogenetic works (Hoyo & Pedrola-Monfort 2006, 2008; Manning & al. 2007; Persson & al. 2011; Vinnersten & Manning 2007; Vinnersten & Rives 2003) did not provide unequivocal grounds for joining of the genera *Colchicum*, *Merendera*, and *Bulbocodium* in one genus.

These genera distinguish to each other by many traits, such as morphological, anatomical (Oganezova 2007), developmental, as well as their chromosome number and ecological preferences.

So important traits as free tepals in the flowers of the species of *Merendera* and a single style in the species of *Bulbocodium* might have evolved secondarily, as a development structure connected to the tendency towards autogamy, so peculiar in these genera. The genus *Androcymbium* with free tepals of the flower could not have been an ancestral taxon for the genera *Merendera* and *Bulbocodium*. The ranges of these taxa do not intersect in the eastern Mediterranean region – a probable place of origin of the genus *Colchicum*, the area of intersection of the ranges of the basalmost species of the genus *Colchicum* and earlier branching Mediterranean species of the genus *Androcymbium*.

New molecular markers and analysis of all known data are necessary to overcome this ambiguity.

The adaptive role of “reversals” in the evolution of the flower structure in the genera *Merendera* and *Bulbocodium* might be connected to the adaptation to the spring time flowering and vegetation, to the lower temperatures and ecologically more complex niches, than those characteristic for the species of *Colchicum*. This condition might be more advantageous in the cases where a mixture of different genes is present, such as cross pollination. Such goal could be achieved easier in the spring time when insects are more active.

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